THE INTERRELATION OF YIELD AND PROTEIN CONTENT OF RANDOM SELECTIONS FROM SINGLE CROSSES IN WHEAT AND BARLEY

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INTRODUCTION

Yield and protein content are the most important characters in Canadian wheat and barley, the former because of its direct effect on the farmer's revenue, and the latter because of its relation to baking quality in wheat and malting and feed value in barley. The inheritance of both these characters is undoubtedly controlled by a number of genetical and environmental factors. Of the two, yield is the more difficult to analyze since, as stated by Worzella (20), it may be regarded as the ultimate expression of all the inherent factors and environmental conditions that have been associated throughout the life of the plant. The analysis of yield can best be carried out by the identification of its component parts, and by a study of their nature, interrelationships, and behavior under varying environmental conditions. The plant breeder is interested primarily in the inherent factors affecting yield, since they represent the components that can be permanently modified by breeding methods. One of these components is protein content.

Examination of data from many sources suggests a definite negative association between yield and protein content of wheat and of barley, part of which association may be attributed to a linkage between the genes for the two characters. It is extremely important that a measure of this association be obtained, since, if it can be proved generally true that varieties which are characterized by high yield tend to be low in protein, then the problem of improvement of malting barley and soft wheats by breeding methods would be greatly simplified. In the case of hard red spring wheats or feed barley, however, where both high yield and high protein content are desired, the attainment of this end is made much more difficult by a genetical relationship such as has been suggested.

This relationship also suggests a simple specific test for the elimination or selection of hybrid strains in early generations of wheat and barley. The problem has been approached by many workers (7, 8, 10, 11, 17) who have attempted to find a means of saving time and work in the selection of improved strains from early-generation hybrid material. The importance of determining a simple means for such a test cannot be over-emphasized, since it is relatively easy to make many crosses which will result in thousands of new genotypes; but it is much more difficult, in the large mass of material, to recognize which strains are valuable and which are worthless. If the negative association between yield and protein content

could be proved true in a sufficiently high proportion of the cases studied, many strains could be discarded in early generations on the basis of a protein determination, thus saving years of tedious work while these strains were increased to a point where enough seed had become available for yield trials.

The purpose for which the following investigation was initiated was to endeavor to establish definitely the relationship which was believed to exist between yielding ability and protein content in wheat and barley.

LITERATURE REVIEW

The negative relationship between yield and protein content has attracted the attention of many workers. Reference to this phenomenon is found in many publications, but unfortunately the problem has, in almost every case, been regarded as an interesting phase of some other project, and has not been investigated thoroughly itself. It is surprising to note the small amount of experimental work which has been carried out on this useful and generally accepted correlation between yield and protein content.

In 1926, Goulden and Elders (6) pointed out that, in wheat improvement, the primary objectives are yield and quality. Yield, in their estimation and in that of Clark and Quisenberry (3), is a complicated character, determined by a series of

lesser physiological and morphological characters. Clark (2) and McCalla and Rose (13) state that the most reliable individual measure of quality in wheat is the crude protein content, which can be determined with a high degree of accuracy on a small quantity of grain. In an F_2 population of Marquis x Hard Federation wheats, Clark (2) found that the crude protein content of the hybrid plants was negatively correlated with yield, the coefficient of correlation being $-.231 \pm .027$. Yield affected the protein content more than any other character studied. These characters included dates of heading and ripening, fruiting period, and height. In two tests conducted on the F_3 plants the correlation coefficients were, respectively, $+.256 \pm .042$ and $-.732 \pm .018$. Clark concludes that there is segregation for crude protein content in wheat hybrids similar to that for other quantitative characters, including yield. Inheritance of crude protein content is as complex as that of yield, and environment has as much effect on the one as on the other. The two characters are frequently, but not always, negatively associated.

Clark and Quisenberry (3), in a study of the yield and protein content of 181 F_2 plants from a Kota x Marquis cross, concluded that there is a slight but not significant tendency for the two characters to be negatively correlated. They did find, however, a significant positive correlation between the crude protein content of F_2 plants and F_3 strains, indicating that, in breeding for high protein content, the

selection of high-protein plants in the segregating F_2 generation offers a promising method of attack.

A different approach to the problem was made by Malloch and Newton (12) who tested the relationship between yield and protein content of single varieties as affected by variations in the soil and in pruning the plants. Fifty rod-row samples were selected at random and analyzed for yield and protein content. The correlation coefficient was -.68 for Red Bobs in 1930, and -.42 for Marquis in 1931. It was also shown that a reduction in yield by pruning resulted in an increase in protein content of the grain. Their conclusion was that there is usually an inverse relation between yield and protein content, though it is not so definite as to mean that yield in all cases can be increased only at the expense of a decrease in the protein content.

In a study of yield and other characters of 25 varieties of hard red spring wheat, Waldron (18) obtained a correlation coefficient of -.556 for yield and protein content, with a regression of yield on protein content of -3.4 bushels. Waldron stresses the economic importance of this relationship, indicating that with a regression as great as this a distinct protein premium on the market would be necessary to recompense the farmer for his high-protein wheat, since the yield of his crop would be decreased.

Whiteside (19) states that in a study of 28 varieties

of spring wheat grown at each of three stations, yield and protein content were not correlated when the effects of station, replication, and variety were removed. No real differences were found between the calculated protein percentages for composite samples made up from the four plots from each station and the percentages obtained by averaging the results from the individual plots. The two sets of protein percentages gave a correlation coefficient of +.9998.

Neatby and McCalla (15) examined yield and protein data secured from hard wheat, soft wheat, and barley variety trials conducted over a period of years at the University of Alberta, together with data obtained on numerous tests in Saskatchewan, Manitoba, Washington, Oregon, and Utah. For 1933 the correlation between the general means of yield and protein for 36 varieties of hard wheat grown at 11 stations was determined. This coefficient, -.55, is almost certainly due largely to genetical causes. When samples of winter wheat from five stations were composited for protein determinations, a yield-protein correlation coefficient of -.57 was obtained. Working with soft wheat data, the general means of yield and protein for 11 varieties at 7 stations were correlated and gave an extremely high correlation coefficient of -.92. A similar procedure applied to barley data indicated that the relation holds also for this crop. The correlation coefficient for the means of yield and protein in this case was -.72. It was con-

cluded that yield and protein content in these cereals have a genetically controlled negative association with each other. Yielding ability and protein content are assumed to be controlled by the same laws of inheritance as are other more obvious characters, subject of course to environmental influences such as moisture, soil nitrogen, and general nutritional conditions. This supports the conclusions of Clark (2). The constancy of these genetical differences for both yield and protein content when the effect of environment is controlled was demonstrated.

McCalla and Rose (13) state that high-protein varieties of wheat are almost invariably low in yield, and suggest that great difficulty would be experienced in an attempt to obtain a high-yielding, high-protein, hard spring wheat.

In their cultural studies with barley, Olson, Meredith, Laidlaw, and Lejeune (16) state that the important objectives from the point of view of both producer and consumer are yield and malting quality. Meredith and Olson (14) point out the importance of protein content in the evaluation of malting quality. The desirability of a low-protein malting barley is stressed again by Anderson, Meredith, and Sallans (1).

MATERIAL AND METHODS

1944

Barley

The cross, Trebi x Peatland, was made in 1936 to provide material for a genetical study of the relationship between yield and protein content. Peatland is characterized by very high protein content and low yield; while Trebi is consistently a high-yielding, low-protein variety. The seed of the cross was grown in bulk plots where it was allowed to increase and segregate till the fall of 1939 when 100 random selections were made of plants carrying F_4 seed.

It was thought that, if the selection of heads was made at random, and if yielding ability and protein content are inherited independently, the samples would show equal numbers of high-yield-high-protein, low-yield-low-protein, high-yield-low-protein, and low-yield-high-protein selections, plus intermediate forms. If, however, the scatter of points obtained by plotting yield in bushels per acre against protein content showed any definite trend, this information might be of value in carrying out future selection work with hybrid populations. An explanation of how this information could be used is illustrated by the correlation surface in Figure 1.

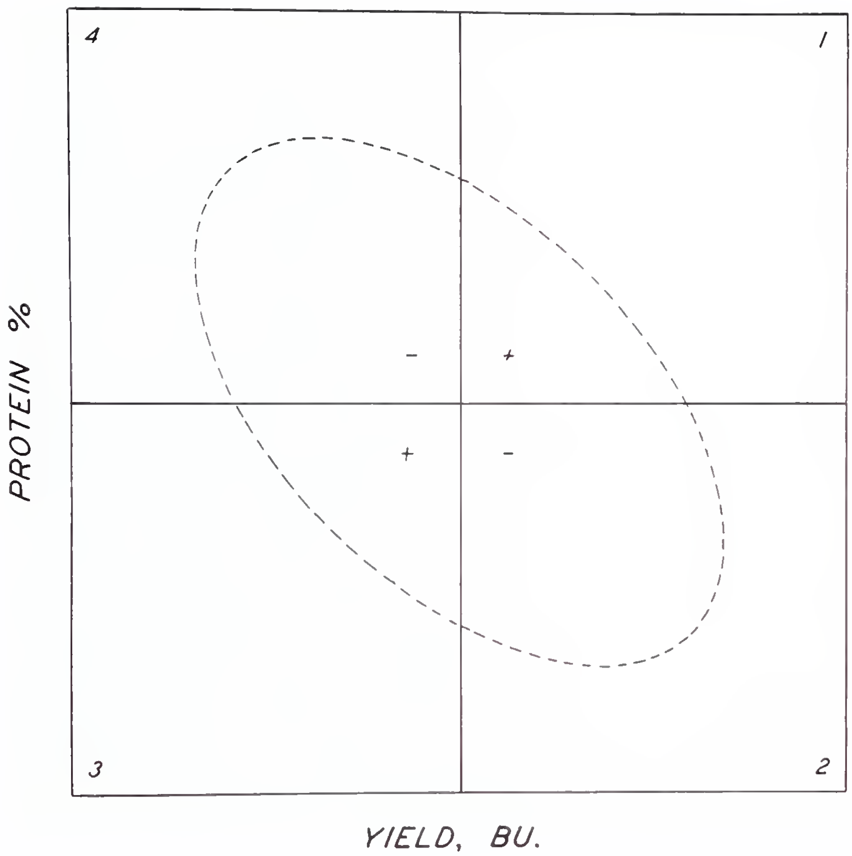

Figure 1

Correlation surface illustrating general association between yield and protein content

If the association shown in Figure 1 could be proved to be generally true, it would then be possible to use a protein determination as a means of selection with small quantities of hybrid seed. The extremely high protein selections could be discarded since they would, in all probability, later prove to be low in yield. If the plants under test were destined to be feed barleys, then those with very low protein content could be discarded for that characteristic alone. In short, for feed barleys, the most desirable segregates are found in quadrant 1, while for malting barleys the best selections would be plotted in quadrant 2. If the association between yield and protein content were known, protein analysis alone could then afford a sufficiently accurate method of selection.

The seed from the 100 plants selected in 1939 was planted in separate rows and increased during 1940. The following spring the 100 F_5 selections were placed in a quadruplicated yield test. Lack of sufficient moisture during the growing season resulted in a poor stand for all selections. The yield results in particular were not thought to be as accurate as would be desired for correlation studies with protein content. The analysis of the protein content of each selection was carried out, however, and the results recorded. Calculations based on the 1941 data give a regression coefficient for yield and protein content that is negative and highly significant (b_{py} = -.037). The regression equation is P = 17.27 -

.037 y. In Figure 2 is presented the scatter of points and the regression line obtained for this test. The simple correlation coefficient is not large but is highly significant (r_{py} = -.300).

In 1944 a yield trial was again grown at Edmonton using seed from the 1940 increase plots. Only 82 selections were included, using a simple randomized block design with four replicates. Replicates were split to form more compact and uniform units. Each plot consisted of three rows, 18.5 feet long, and 9 inches apart, sown at the rate of 2 bushels per acre. Seeding was done with a V-belt seeder. No fertilizer was added.

Field notes were taken on heading date and growth period (days from seeding to maturity). At maturity the centre row of each plot was trimmed to 16.5 feet to minimize any border effect from the open pathways. Each centre row was cut by hand and wrapped in a cotton wrapper to prevent mixing and loss of seed. Each sheaf was threshed in a rod-row thresher, and the yield recorded. Protein analysis was carried out on composite samples of seed from the four replicates, a method considered satisfactory by Whiteside (19).

Analysis of variance was applied to the yield but not to the protein data.

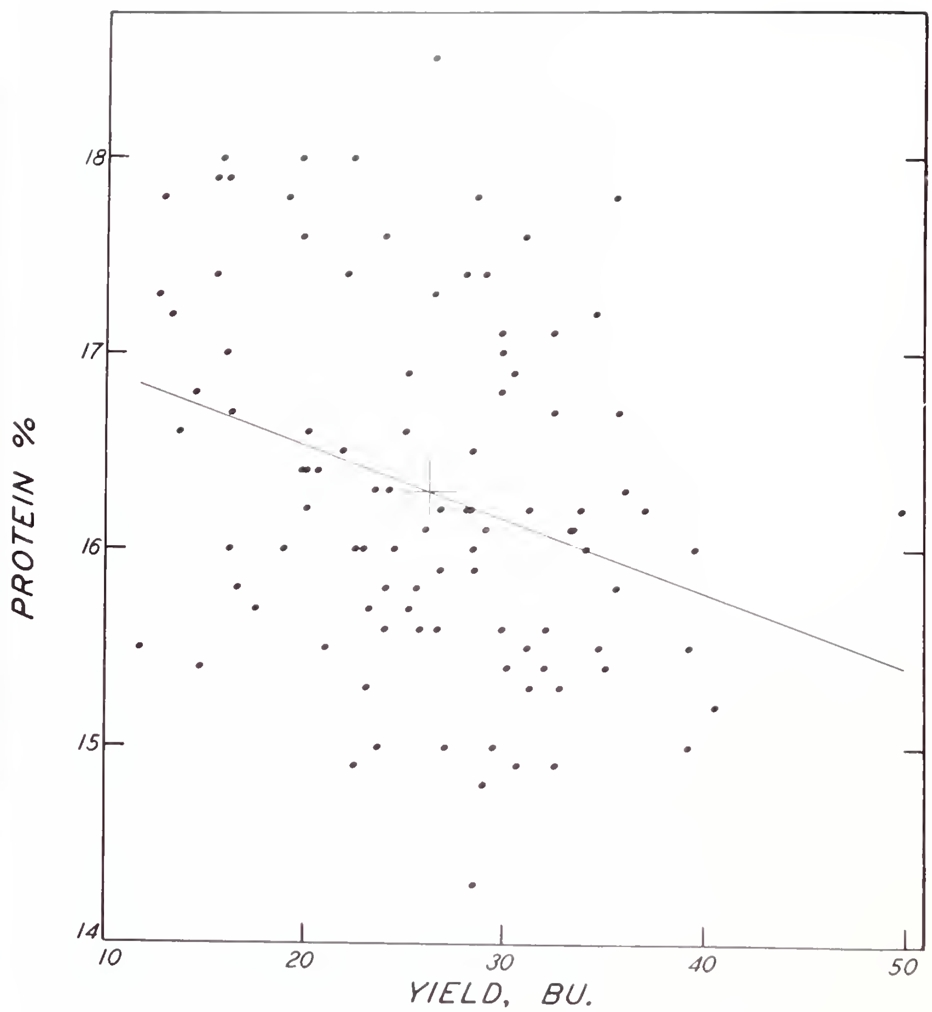

Figure 2

Relation between yield and protein content
in the 1941 barley test

Wheat

The cross selected for study of the yield-protein relationship was Bunyip x Dicklow. Both parents are soft wheats. Bunyip is characterized by high protein and low yield, while Dicklow is noted for low protein and high yield. The hybrid seed was grown in bulk plots till the F_4 generation in 1940 when random selections of plants were made. These selections were increased during 1941. Yield trials were carried out in 1944 at both Edmonton (black soil) and Fallis (gray soil) using seed of 100 selections from the increase plots of 1941.

The field plot design was of the incomplete block type, known as the simple lattice, and illustrated by Cox and Eckhardt (4) and Hayes and Immer (9). Since the number of selections forms a perfect square and $v = k^2$, v (varieties) equals 100, and k (blocks) equals 10. The 100 selections were arranged in incomplete blocks, each block containing 10 selections. There were four replicates, each made up of 10 blocks. The improved efficiency of the lattice design over simple randomized blocks has been established where large numbers of selections are to be used, as shown by Cox and Eckhardt (4).

These plots, like those for the barley, consisted of 3 rows, 18.5 feet long and 9 inches apart, but were sown at the rate of 1.25 bushels per acre. No fertilizer was added at either station.

Field notes were taken at Edmonton, but not at Fallis, on heading date and growth period. The centre row of each plot was trimmed to 16.5 feet at maturity, cut by hand, wrapped, and threshed separately in a rod-row thresher. The yield was recorded.

The analysis of variance for yield data was applied in the manner outlined by Hayes and Immer (9).

Protein content was determined on composite samples of seed from the four replicates. No analysis of variance, therefore, could be applied.

1945

Barley

The yield trial, with certain changes, was repeated in 1945. Seed was obtained from the 82 F_6 selections in the 1944 test, and to these were added 18 F_6 selections from the 1941 test. This increased the number of selections to 100, thus making possible the use of the simple lattice design of Cox and Eckhardt (4), which had proved satisfactory for the wheat tests in the previous year. The seeding methods were the same as those outlined for 1944.

At harvest time it was decided that the seed from each plot would be bagged separately, and that protein content

would be determined for each sample. This made possible the use of analysis of variance methods for the protein as well as the yield and growth period data, and also gave the opportunity to apply a correction factor to the mean values for each selection before correlation studies were attempted.

Wheat

The two wheat tests were repeated in 1945, one on the black soil at Edmonton, and the other on the gray soil at Fallis. The seed was taken from the F_7 selections which had been grown during 1944.

At harvest the seed from each plot was placed in individual bags, and protein content determined for each sample. Analysis of variance methods were applied to the yield, protein, and growth period data, and correction factors were used in every case before correlation studies were begun.

EXPERIMENTAL RESULTS

Barley

1944

For the months of May, June, and July, the total precipitation exceeded 11 inches. With this ample supply of moisture all the barley selections exhibited a heavy growth. At heading time the selections showed notable differences in height, straw strength, and earliness, indicating the segregation which these characters and presumably others, including yielding ability and protein content, had undergone during the preceding generations. The agronomic differences are apparent in Figure 3.

The results of the analysis of variance for yield and for growth period are presented in Table I. In the case of yield highly significant differences were obtained for both selections and replicates. For growth period highly significant differences were found for selections but not for replicates. Analysis of variance could not be applied to the protein data, since protein determinations were carried out on composite samples from the four replicates.

Figure 3

Partial view of 1944 barley test, showing agronomic differences between selections

TABLE I

Results of the analysis of variance for yield and growth period of barley selections - 1944

		Mean squares	
Variance due to	D.F.	Yield	Growth period
Selections	81	558.3**	99.7**
Replicates	3	801.6**	3.7
Error	244	148.0	6.7
Total	328		

** Exceeds the 1% point.

Figure 4 shows the relationship between yield in bushels per acre and protein content in percent. The slope of the regression line is indicated by a b_{py} value of -.044, a highly significant value. The regression equation for protein in terms of yield is P = 17.26 - 0.044 y. Thus a gain of 1% in protein is obtained in this case through a decrease of 22 bushels per acre in yield.

Growth period exhibits a definite influence upon the relationship between yield and protein content, as indicated by a partial regression coefficient of $b_{py.m}$ = -.056. When the effect of growth period is eliminated, the regression line becomes steeper and a change in protein content of 1% is accompanied by a change in yield of only 18 bushels per acre.

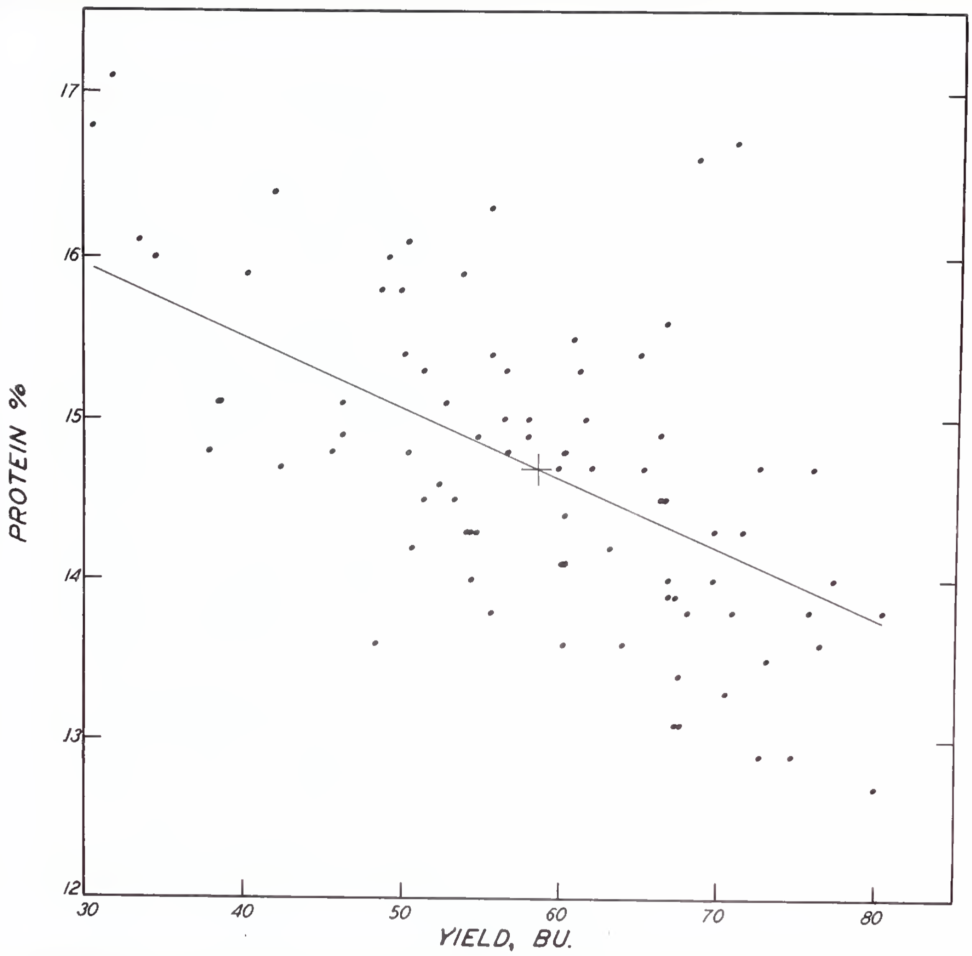

Figure 4

Relation between yield and protein content
in the 1944 barley test

The association between yield and protein content is measured by the correlation coefficient r_{py} which has a highly significant value of -.533. This compares very closely with the results obtained by Waldron (18). Protein content and growth period were not found to be correlated to a significant degree. Yield and growth period, however, gave a highly significant correlation coefficient of -.356. This negative association between yield and growth period was hardly expected, for this means that the earliest selections were the highest in yield. When growth period was held constant, the partial correlation coefficient $r_{py.m}$ had a value of -.644. Thus, the association between protein content and yield was improved by considering it independent of the effect of the length of the growth period.

The multiple correlation coefficient, $R_{p.ym} = .764$, also was highly significant, and proved highly significantly greater than $r_{py} = -.533$, when tested by the method illustrated by Goulden (5).

A summary of the regression and correlation coefficients is included in Table III.

1945

The growing season for 1945 was extremely dry. Only 4.74 inches of rain fell during May, June, and July. The month of May contributed only 0.26 inches of rainfall to this

total. All the plots grew well and maintained an erect stand which was conducive to both easy and accurate harvesting operations. Differences in height, days to heading, and growth period could easily be distinguished, as is shown by Figures 5 and 6.

Results of the analysis of variance for yield, protein content, and growth period are presented in Table II. Highly significant differences were obtained for both selections and replicates in all three cases.

TABLE II

Results of the analysis of variance for yield, protein content, and growth period of barley selections, 1945

		Mean squares		
Variance due to	D.F.	Yield	Protein	Growth period
Selections	99	514.06**	3.80**	146.5**
Replicates	3	4851.70**	4.83**	188.0**
Error	297	57.73	0.33	2.7
Total	399			

** Exceeds the 1% point.

The relationship between yield and protein content for 1945 is shown in Figure 7. Considering the difference in precipitation for 1944 and 1945, it is surprising to note that the range of yields for both years is approximately the same.

Figure 5

Partial view of 1945 barley test,
showing agronomic differences
between selections

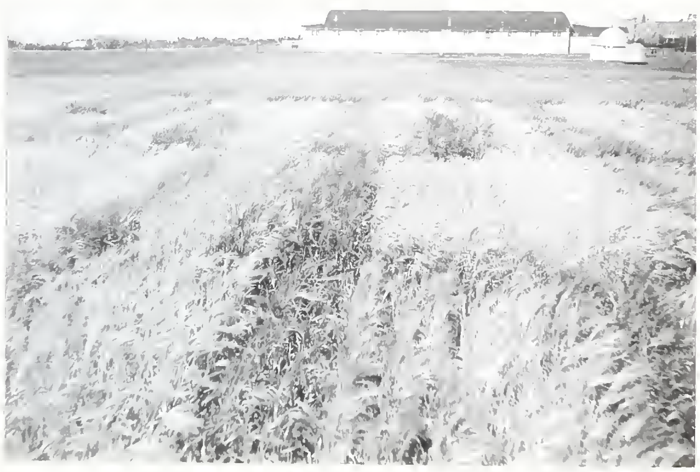

Figure 6

Partial view of 1945 barley test, showing agronomic differences between selections

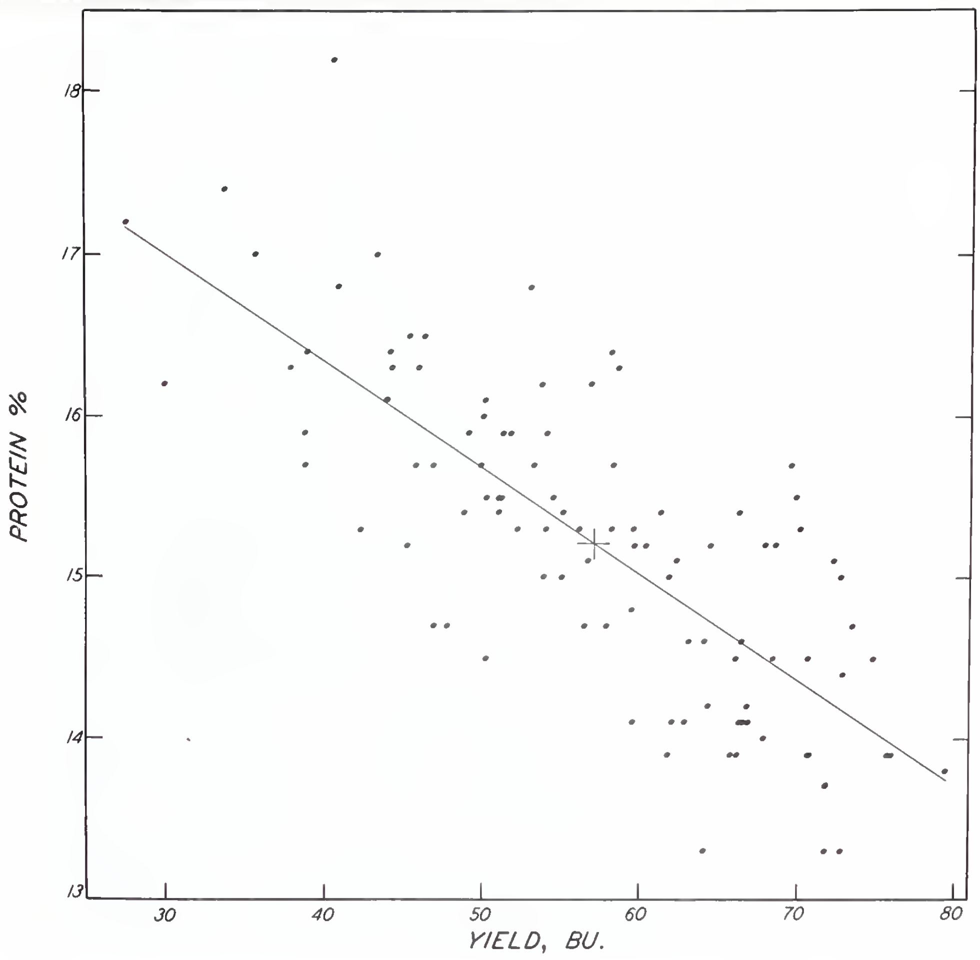

Figure 7

Relation between yield and protein content in the 1945 barley test

The range of protein values is also similar, though, as would be expected, the 1945 range lies slightly higher. The slope of the regression line is steeper than for 1944, the b_{py} value being -.066 (highly significant). A decrease of 15 bushels per acre in yield would in general mean a 1% increase in protein content. The regression equation is $P = 19.0 - 0.066\ y$. The length of the growth period showed very little effect upon the yield-protein relationship. The partial regression coefficient, $b_{py.m} = -.064$, is not significantly different from the simple regression coefficient. The important point is that even for years showing wide climatic differences the general relationship of yield and protein content is of approximately the same order.

A closer association between yield and protein content for 1945 as compared with 1944 is indicated by a higher correlation coefficient, $r_{py} = -.761$ (highly significant). The results for 1944 are therefore not only substantiated, but improved upon, by the results for 1945. This also holds for the association between protein content and growth period, which in 1944 was negative though not significant, and in 1945 gave a negative correlation $r_{pm} = -.524$, which was highly significant. Yield and growth period gave contradictory results for the two years, the correlation coefficient for 1945 being positive and highly significant, $r_{ym} = +.679$. This positive correlation coefficient was more to be expected than the nega-

tive one of the previous year and, considering the almost ideal harvesting conditions, is probably the more nearly correct figure. The explanation for the 1944 result may lie in the fact that the early varieties were harvested while still standing erect and without undue loss of grain through handling, while the late varieties were harvested under adverse conditions caused by lodging. In the 1945 crop, on the other hand, all the selections were erect and thus were not subject to error through mechanical loss of grain at harvest. A further explanation for the negative association between yield and growth period in 1944 may be the possibility that the early, erect selections had more completely filled spikes and, consequently, gave higher yields.

When the effect of growth period was eliminated the degree to which yield and protein content varied together was not improved, but dropped to the value $r_{py.m} = -.649$, which was still highly significant. This value compares very closely to the partial correlation coefficient for 1944, $r_{py.m} = -.644$.

The multiple correlation coefficient also is very similar to the 1944 figure with a value of $R_{p.ym} = .762$ (highly significant). This value is not significantly higher than the simple correlation coefficient, $r_{py} = -.761$.

A summary of the regression and correlation coefficients is included in Table III.

Means of Two Tests

When the means of yield and protein content for the two years were calculated and plotted, the scatter presented in Figure 8 was obtained. The regression coefficient, b_{py} = -.074, was highly significant. The correlation coefficient was also highly significant, with a value for r_{py} of -.737.

Interyear

Figure 9 presents the scatter of points which is the result of plotting 1945 yield against 1944 protein content. The slope is far from steep, but the regression coefficient is highly significant, b_{py} = -.032. The association between yield and protein content is not striking, but the general negative trend is apparent. A highly significant correlation coefficient, r_{py} = -.366, was obtained. Considering the wide differences in growing conditions for the two tests from which these data were drawn, a correlation coefficient of any larger value would not be expected.

Plotting 1944 yield against 1945 protein content gave the scatter of points depicted in Figure 10. Significant results were not obtained in this case for either the regression or the correlation coefficient. The indication is that extreme differences in precipitation for the two years resulted in highly dissimilar responses each year from many of the

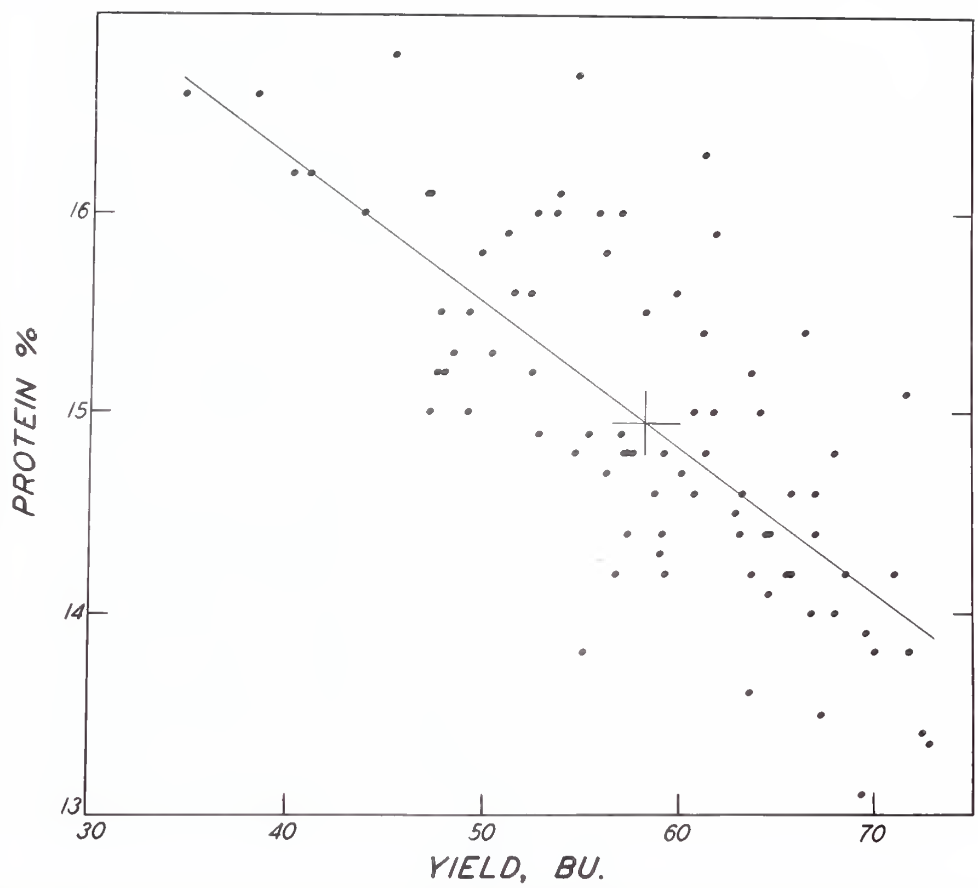

Figure 8

Relation between yield and protein content, using the means calculated from the 1944 and 1945 barley tests

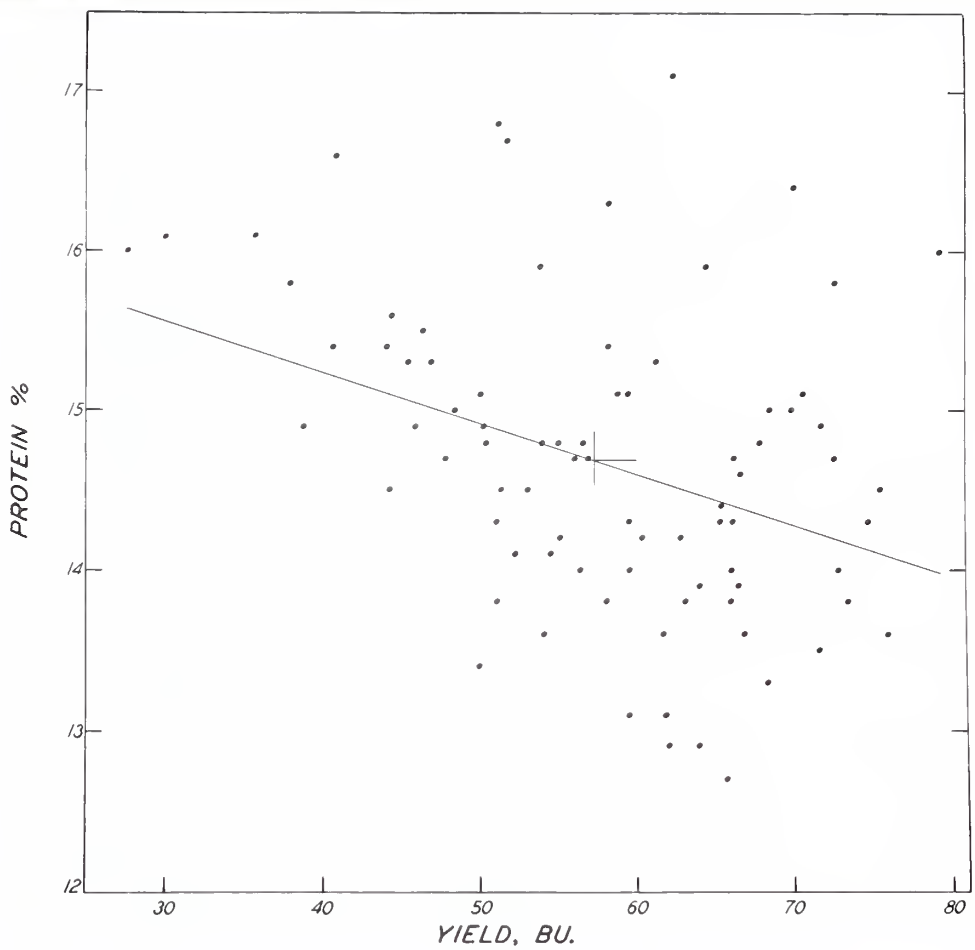

Figure 9

Relation between 1945 yield and
1944 protein content in
the barley tests

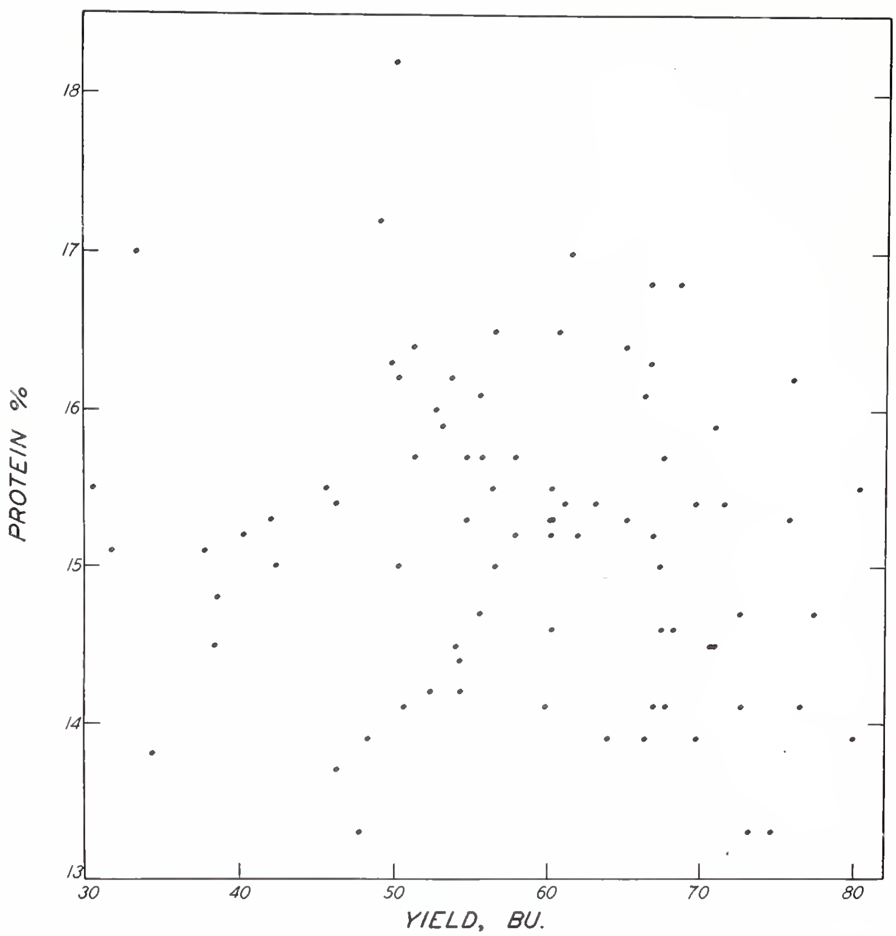

Figure 10

Relation between 1944 yield and
1945 protein content in
the barley tests.

selections. The exhibition of this phenomenon does not come as a complete surprise, since differential responses to changes of climate--particularly available moisture--have been noticed between standard varieties in past years.

A summary of the regression and correlation coefficients for all barley data is presented in Table III.

TABLE III

Summary of regression and correlation coefficients for barley data, 1944 and 1945

	1944	1945	Based on 2-test means
b_{py}	-.044**	-.066**	-.074**
$b_{py.m}$	-.056**	-.064**	
r_{py}	-.533**	-.761**	-.737**
r_{pm}	-.170	-.524**	
r_{ym}	-.356**	+.679**	
$r_{py.m}$	-.644**	-.649**	
$R_{p.ym}$	.764**	.762**	

Interyear

	1945 yield/1944 protein	1944 yield/1945 protein
b_{py}	-.032**	-.011
r_{py}	-.366**	-.136

Wheat

1944

Edmonton (Black soil)

The 1944 wheat yield-protein test showed very heavy growth in all plots, and in general was late in maturing. Differences in height, days to heading, and growth period could easily be seen. Several heavy rains during the growing season resulted in considerable lodging. Fortunately very little second-growth appeared.

In the analysis of variance for yield data, highly significant differences were shown for selections, and significant differences for replicates. Growth period data gave highly significant differences for both selections and replicates. The results of analysis of variance for both these characters are presented in Table IV. Composite samples from four replicates were used for obtaining the protein results, thus making analysis of variance for protein content impossible.

Figure 11 presents a scatter of 100 points, which indicates the relationship between yield in bushels per acre and protein content in percent for the wheat test at Edmonton in 1944. The regression coefficient is negative and highly significant, $b_{py} = -.053$. With a

change of 19 bushels per acre in yield there is a corresponding change in protein content of approximately 1%. The regression equation is $P = 15.18 - 0.053\ y$.

TABLE IV

Results of the analysis of variance for yield and for growth period of wheat selections, Edmonton, 1944

Variance due to	D.F.	Mean squares	
		Yield	Growth period
Selections	99	754.09**	6.38**
Replicates	3	447.19*	74.06**
Error	297	126.49	1.57
Total	399		

** Exceeds the 1% point
* Exceeds the 5% point.

The negative and highly significant correlation coefficient, $r_{py} = -.806$, is the highest obtained for any of the tests carried out. This measure shows a high degree of association between the two characters. It indicates that in general there is only a very small chance of obtaining a high-yield, high-protein selection. However, the possibility of obtaining a high-yield, low-protein segregate is greatly enhanced. This is a very encouraging feature from the point of view of the soft-

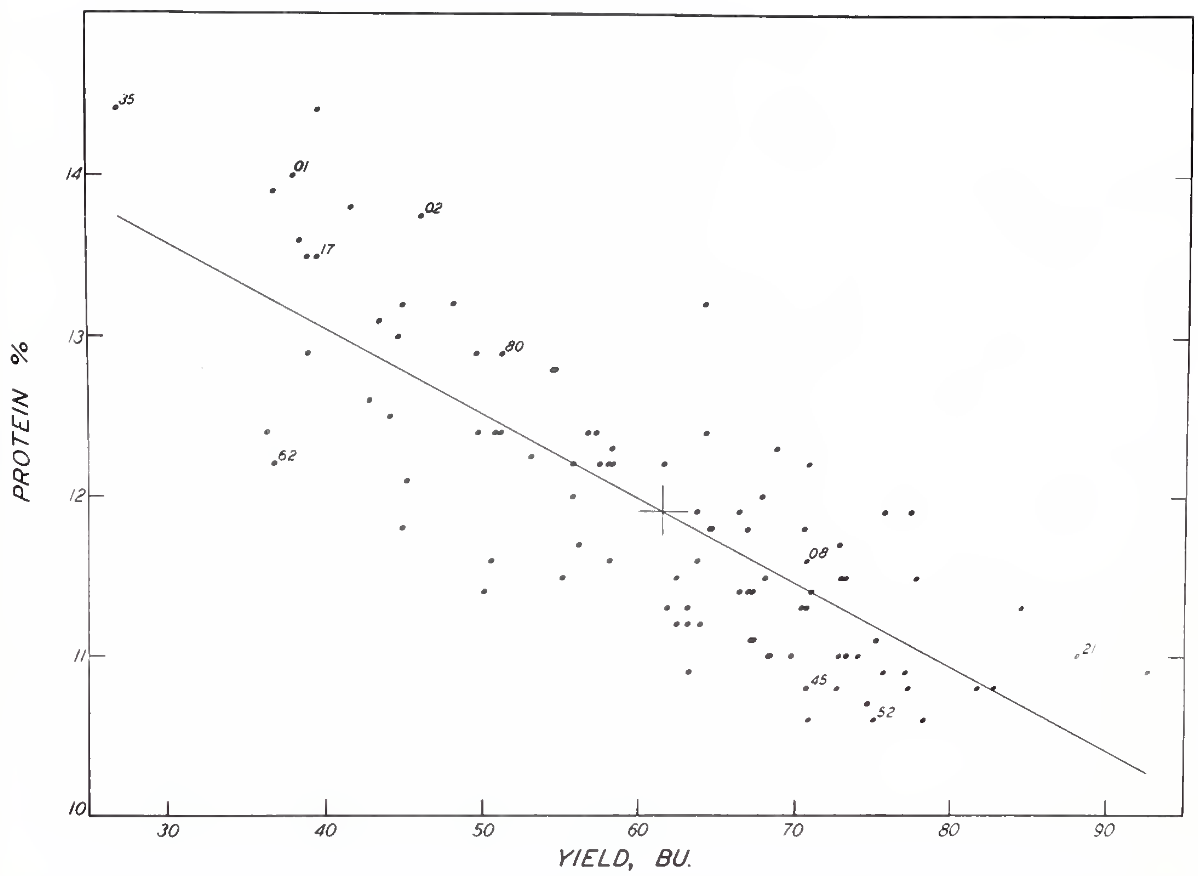

Figure 11

Relation between yield and protein
content in the 1944 wheat
test, Edmonton

wheat breeder, who is naturally interested in high yields, and at the same time desires varieties of low protein content.

The correlation coefficient for protein content and days to maturity is rather surprising in that it is the opposite sign to that obtained for the barley tests of both years. Its value is +.423 (highly significant). It has generally been considered true that early varieties show the highest protein content, but this belief is not borne out in this case. This result was perhaps inevitable with this series since the protein-yield association is high and the yield-growth period association is the opposite of that usually expected.

The correlation coefficient for yield and growth period is negative and highly significant, $r_{ym} = -.480$. This is in accord with the result obtained in the barley test of the same year, but the association of high yield with a short growing period is contrary to the general expectation. When growth period is held constant the partial correlation coefficient is $r_{py.m} = -.758$. This figure is highly significant, but is slightly lower than the simple correlation coefficient $r_{pm} = -.806$.

The multiple correlation coefficient expressing the combined association of yield and growth period with

protein content is $R_{p.ym} = .806$, which is exactly the same value as the simple correlation coefficient for yield and protein content. No increase in information on the association of greatest interest is obtained, therefore, by considering growth period data.

A summary of the regression and correlation coefficients for the Edmonton wheat test in 1944 is included in Table VIII.

<u>Fallis (Gray soil)</u>

The Fallis test for 1944 was excellent in all respects. An ample supply of moisture resulted in a heavy stand of grain which showed no tendency to lodge throughout the entire season. It was thus possible to carry out harvesting operations with the minimum amount of mechanical error.

Since this test was located a considerable distance from Edmonton, continuous observation was impossible, with the result that notes on growth period were not taken. The results of the analysis of variance for yield data are presented in Table V. Highly significant differences were obtained for both selections and replicates.

Yield in bushels per acre was plotted against protein content in percent, and the resulting scatter is

presented in Figure 12. A steep regression line is indicated by the highly significant regression coefficient, $b_{py} = -.091$. In general, an increase in yield of only 11 bushels per acre results in a drop in protein content of 1%. It is interesting to compare these figures with those obtained for Edmonton where the increase in yield must be twice as much to give the same decrease in protein content. The explanation is no doubt found in the relative scarcity of available nitrogen in the gray wooded soils. The regression equation is $P = 11.77 - 0.091\ y$.

TABLE V

Results of the analysis of variance
for yield of wheat selections,
Fallis, 1944

Variance due to	D.F.	Yield mean squares
Selections	99	155.37**
Replicates	3	1215.32**
Error	297	34.58
Total	399	

** Exceeds the 1% point.

The association between yield and protein content is not as close as for the Edmonton test, but is nevertheless highly significant, $r_{py} = -.666$. A few of

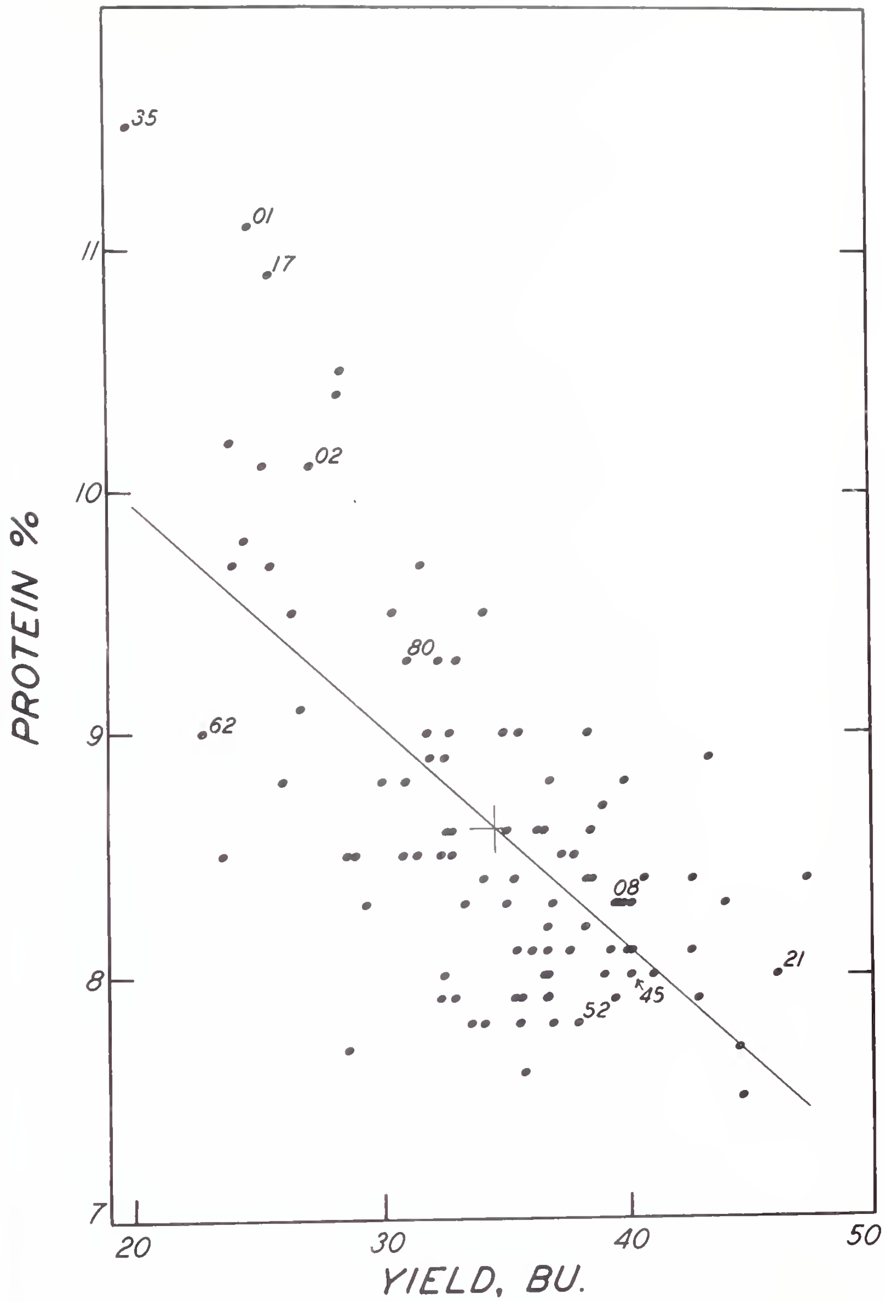

Figure 12

Relation between yield and protein content in the 1944 wheat test, Fallis

the points have been tagged with the numbers of the selections they represent in order that a comparison may be made with the performance of the same varieties at Edmonton. All the points for both stations were compared at the time these few were tagged and there was found to be a striking similarity in the general position of the points. Some differences in performance occurred but, in a high proportion of the cases, the response of the selection was very similar whether grown on black or gray soil. Examination of yield and protein data in Table IX will substantiate this statement.

1945

Edmonton (Black soil)

The wheat test at Edmonton in 1945 was grown under adverse climatic conditions. A very dry spring led to uneven germination, the effect of which remained evident throughout the entire growing season. No lodging appeared in any of the plots.

For each plot data were recorded on yield, protein content, and growth period. Analysis of variance methods were applied to the data in all three cases and the results appear in Table VI. Highly significant differences were found for selections and replicates in each case.

TABLE VI

Results of the analysis of variance for yield, protein content, and growth period of wheat selections, Edmonton, 1945

		Mean squares		
Variance due to	D.F.	Yield	Protein	Growth period
Selections	99	156.36**	1.07**	25.2**
Replicates	3	1527.95**	5.59**	86.0**
Error	297	61.62	0.26	5.5
Total	399			

** Exceeds the 1% point

Yield in bushels per acre is plotted against protein content in percent in Figure 13. The b_{py} value is -.048 (highly significant). This slope compares very closely with that obtained in the 1944 test, an increase of 21 bushels per acre in yield being accompanied by a loss of 1% in protein content. The regression equation is $P = 16.1 - 0.048\ y$. The influence of growth period upon the yield-protein relationship is indicated by the partial regression coefficient, $b_{py.m} = -.058$. When growth period is held constant the regression line for yield and protein content assumes a steeper slope.

The correlation coefficient for yield and protein content is negative and highly significant, r_{py} =

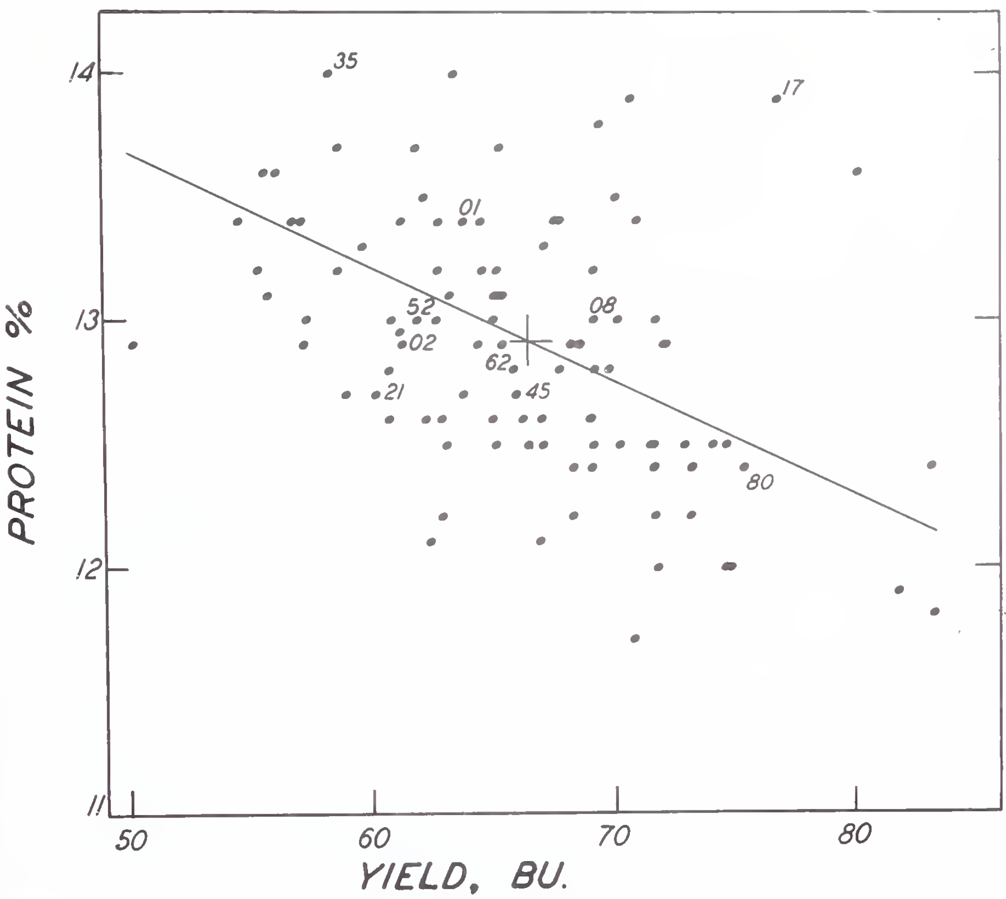

Figure 13

Relation between yield and protein content in the 1945 wheat test, Edmonton

-.527. The degree of association between the two characters is not equal to that of either of the tests in 1944, but this may be due in some measure to the variation in yields caused by adverse seeding and growing conditions. In general, the correlation shown by the scatter of points is good.

The positive correlation between protein content and growth period for 1944 is substantiated by a similar figure for 1945, r_{pm} = +.265. This figure is highly significant.

The association between yield and growth period in 1945, in line with that obtained for the barley test, is contrary in sign to the result for 1944. The correlation coefficient is positive and highly significant, r_{ym} = +.255. The association of higher yields with the later-maturing selections is more to be expected than the negative correlation of 1944.

The association between yield and protein content is improved when growth period is held constant, as evidenced by the value $r_{py.m}$ = -.638 (highly significant).

The combined effect of yield and growth period on protein content also gives a highly significant figure, $R_{p.ym}$ = .670. This value is highly significantly greater than the simple correlation coefficient, r_{py} = -.527.

A summary of the regression and correlation coefficients is included in Table VIII.

Fallis (Gray soil)

A comparatively dry growing season resulted in a lighter stand of plants than was obtained in 1944.

The results of analysis of variance for yield and for protein content are presented in Table VII. Highly significant differences were demonstrated for both selections and replicates in each case. No data were recorded for growth period, since the location of the test made continuous observation impossible.

TABLE VII

Results of the analysis of variance for yield and for protein content of wheat selections, Fallis, 1945

		Mean squares	
Variance due to	D.F.	Yield	Protein
Selections	99	91.55**	1.39**
Replicates	3	225.58**	39.48**
Error	297	47.19	0.78
Total	399		

** Exceeds the 1% point.

The scatter of points obtained by plotting yield against protein content is presented in Figure 14. The regression coefficient, b_{py} = -.079, is highly

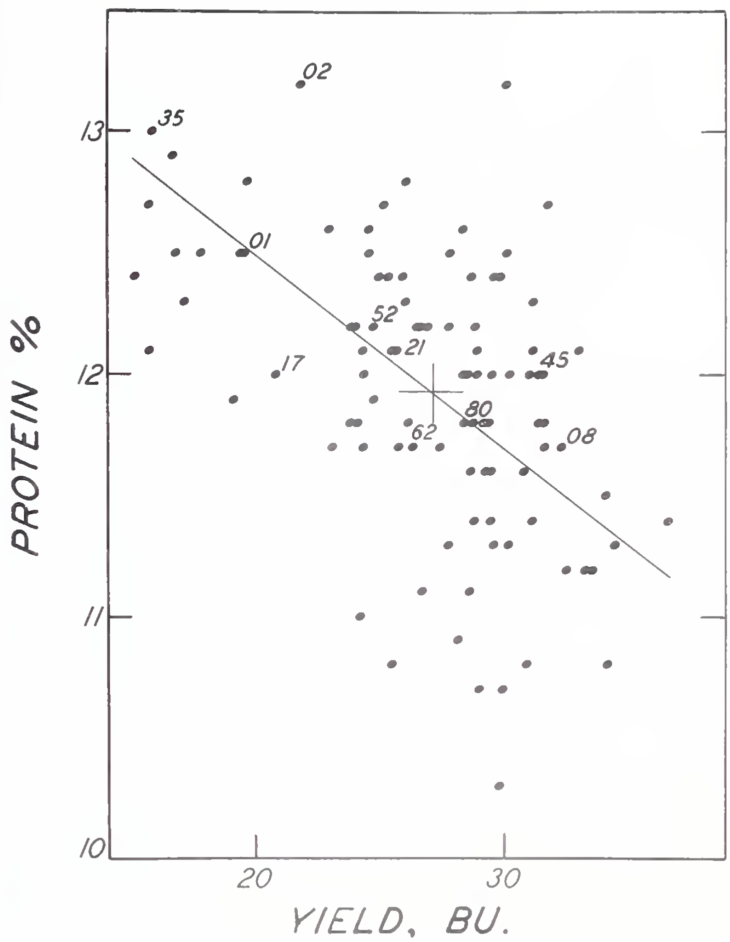

Figure 14

Relation between yield and protein
content in the 1945 wheat
test, Fallis

significant. The slope is not as steep as that for the 1944 test, but is still above any obtained for tests grown on Edmonton soil. The belief that a scarcity of available nitrogen plays an important part in the yield-protein relationship at Fallis is substantiated. The regression equation is $P = 14.07 - .079\ y$.

The association between yield and protein content is essentially the same as that obtained at the same station in 1944. The correlation coefficient is highly significant, $r_{py} = -.641$.

<u>Means of Four Tests</u>

The mean values for yield and for protein content were calculated, using the data from the four wheat tests. The relationship between these mean values is shown in Figure 15.

The regression coefficient, $b_{py} = -.072$, is highly significant. The correlation coefficient is also highly significant, $r_{py} = -.750$. Environmental effect has been greatly reduced by use of this procedure, and the association shown by the correlation coefficient is due almost entirely to genetical reasons.

A summary of the regression and correlation coefficients for the wheat tests at Edmonton and Fallis, in 1944 and 1945, is presented in Table VIII.

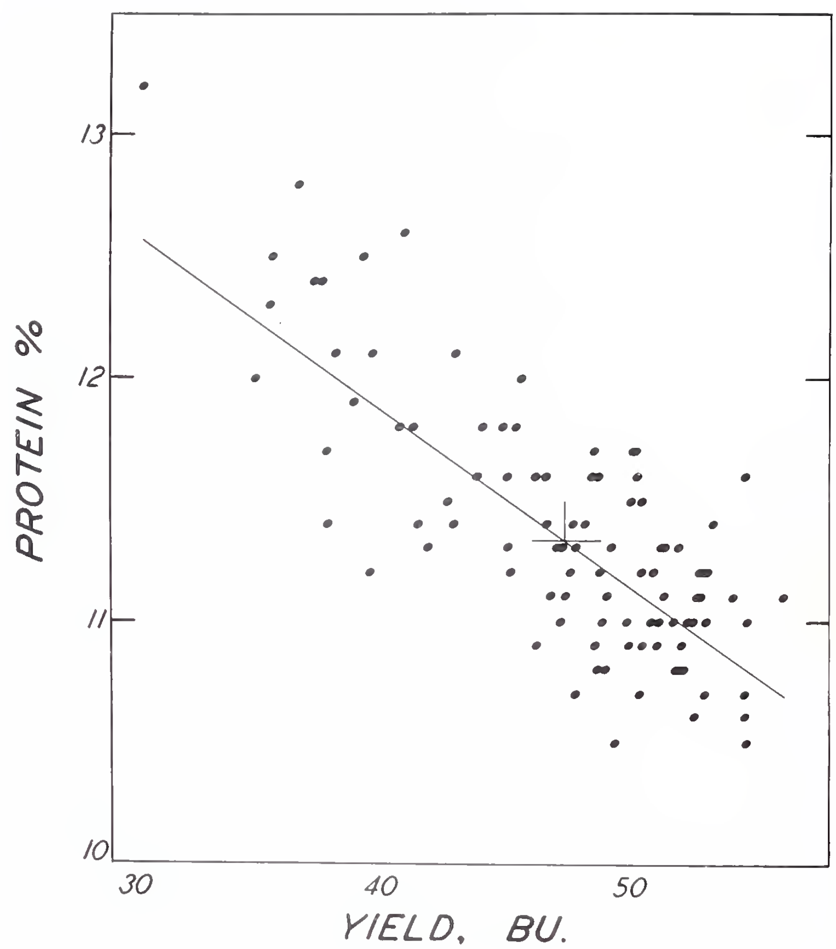

Figure 15

Relation between yield and protein content, using the means calculated from the four wheat tests

TABLE VIII

A summary of regression and correlation coefficients for wheat tests at Edmonton and Fallis, in 1944 and 1945

	1944		1945		
	Edmonton	Fallis	Edmonton	Fallis	Based on 4-test means
b_{py}	-.053**	-.091**	-.048**	-.079**	-.072**
$b_{py.m}$	--	--	-.058**	--	--
r_{py}	-.806**	-.666**	-.527**	-.641**	-.750**
r_{pm}	+.423**	--	+.265**	--	
r_{ym}	-.480**	--	+.255**	--	
$r_{py.m}$	-.758**	--	-.638**	--	
$R_{p.ym}$	.806**	--	.670**	--	

** Exceeds the 1% point.

A summary of yield and protein data for Edmonton and Fallis, 1944, together with the mean values for each selection calculated from four tests, is presented in Table IX.

TABLE IX

Summary showing: yield and protein data for Edmonton and Fallis, 1944; and mean values calculated from four tests

	1944					
	Edmonton		Fallis		Means of 4 tests	
Selection number	Yield (bu./ac.)	Protein (%)	Yield (bu./ac.)	Protein (%)	Protein	Yield
07	84.7	11.3	44.0	8.3	11.2	56.2
21	88.2	11.0	45.0	8.1	11.0	54.8
68	70.5	11.3	36.7	8.0	10.5	54.8
46	66.5	11.9	43.4	8.9	11.6	54.7
51	74.8	10.7	42.9	7.9	10.6	54.6
58	81.7	10.8	35.7	7.8	10.7	54.6
87	92.6	10.9	32.9	8.5	11.1	54.2
95	75.9	11.9	40.7	8.4	11.4	53.4
32	74.1	11.0	42.7	8.4	11.2	53.3
27	78.2	10.6	36.3	8.6	11.0	53.2
08	70.9	11.6	39.8	8.3	11.2	53.1
39	75.7	10.9	36.8	7.9	10.7	53.1
37	92.7	11.4	28.7	8.5	11.1	52.9
81	64.3	13.2	33.6	7.8	11.2	52.8
12	69.8	11.0	46.2	8.0	11.1	52.7
11	70.8	11.3	39.5	7.9	11.0	52.6
18	63.2	10.9	44.5	7.7	10.6	52.6
67	73.4	11.5	38.4	9.0	11.0	52.4
09	58.3	12.3	44.7	7.5	10.8	52.3
45	70.8	10.8	40.2	8.0	10.9	52.2
92	73.4	11.0	35.4	7.9	10.8	52.1
41	82.8	10.8	38.6	8.4	10.8	52.0
48	70.7	11.8	38.5	8.6	11.3	52.0
71	72.9	11.0	37.8	8.5	11.0	51.8
93	77.5	11.9	39.3	8.1	11.3	51.5
53	68.5	11.0	38.3	8.2	11.3	51.4
76	56.8	12.4	36.1	8.1	11.1	51.4
42	63.1	11.3	40.2	8.3	11.0	51.2
30	51.3	12.4	33.0	7.9	10.9	51.1
83	77.9	11.5	28.7	7.7	11.2	51.0
64	75.2	11.1	32.6	8.9	11.2	51.0
44	73.0	11.5	35.4	8.4	11.0	50.9
84	68.8	12.3	35.0	9.0	11.5	50.5
00	68.5	11.0	37.0	8.3	10.9	50.5
56	77.1	10.9	39.5	8.3	11.2	50.5
61	56.3	11.7	37.0	7.8	10.7	50.4

TABLE IX (continued)

Selection number	1944 Edmonton Yield (bu./ac.)	1944 Edmonton Protein (%)	1944 Fallis Yield (bu./ac.)	1944 Fallis Protein (%)	Means of 4 tests Protein	Means of 4 tests Yield
47	67.3	11.1	33.1	9.3	11.6	50.3
78	58.4	12.2	37.7	8.1	10.7	50.3
96	68.1	11.5	39.8	8.3	11.2	50.2
66	68.0	12.0	40.2	8.1	11.2	50.2
55	77.2	10.8	39.1	8.0	11.0	50.1
52	75.1	10.6	38.0	7.8	10.9	50.0
31	58.1	12.2	36.9	8.8	11.0	49.9
26	70.9	10.6	35.7	7.9	10.5	49.4
43	73.0	11.7	33.4	8.3	11.3	49.3
63	64.6	11.8	32.4	7.9	11.1	49.1
49	55.2	11.5	35.8	7.6	10.8	49.0
54	72.8	10.8	35.1	8.3	11.0	48.9
77	66.5	11.4	39.6	8.3	11.2	48.8
22	61.7	12.2	36.7	8.6	11.6	48.8
98	62.5	11.5	34.1	8.4	10.8	48.7
23	67.4	11.1	36.8	8.0	10.8	48.7
73	71.0	12.2	37.4	8.5	11.7	48.6
34	71.1	11.4	32.4	8.5	10.9	48.6
15	50.8	12.4	47.3	8.4	11.6	48.5
65	57.3	12.4	35.5	8.1	11.4	48.2
86	63.7	11.9	35.5	8.1	11.3	47.8
25	62.5	11.2	36.8	8.1	10.7	47.8
90	67.1	11.4	32.9	8.6	11.4	47.7
03	55.9	12.0	42.6	8.1	11.2	47.6
14	62.4	11.3	39.9	8.7	11.1	47.4
59	63.1	11.2	34.1	7.8	11.0	47.2
70	57.2	12.2	41.0	8.0	11.3	47.2
85	64.4	12.4	32.5	8.0	11.3	47.0
57	67.3	11.4	31.9	9.0	11.1	46.7
99	63.8	11.6	35.1	8.6	11.4	46.6
80	51.3	12.9	31.1	9.3	11.6	46.6
74	45.0	13.2	36.8	8.2	11.1	46.2
69	50.6	11.6	31.0	8.8	10.9	46.2
40	54.6	12.8	30.5	9.5	12.0	45.6
05	64.6	11.8	30.9	8.7	11.8	45.3
75	64.0	11.2	30.9	8.5	11.2	45.1
82	54.8	12.8	29.0	8.5	11.3	45.0
72	44.6	13.0	38.3	8.4	11.6	45.0
04	67.0	11.8	30.2	8.9	11.6	45.0
60	48.2	13.2	32.4	9.3	11.8	44.8

TABLE IX (continued)

Selection number	1944 Edmonton Yield (bu./ac.)	Edmonton Protein (%)	Fallis Yield (bu./ac.)	Fallis Protein (%)	Means of 4 tests Protein	Means of 4 tests Yield
16	55.9	12.2	31.4	8.5	11.8	44.0
29	57.6	12.2	29.4	8.3	11.6	43.8
79	41.7	13.8	31.7	9.7	12.1	42.9
19	46.5	11.8	32.7	8.6	11.4	42.8
36	39.0	12.9	34.2	9.5	11.5	42.6
20	58.2	11.6	23.7	8.5	11.3	41.8
33	50.1	11.4	26.1	8.8	11.4	41.4
97	53.2	12.2	26.8	9.1	11.8	41.2
17	39.6	13.5	25.7	10.9	12.6	40.8
10	45.4	12.1	32.0	8.8	11.8	40.6
24	38.9	13.5	28.5	10.5	12.1	39.6
13	36.3	12.4	25.6	9.7	11.2	39.5
02	46.2	13.7	27.2	10.1	12.5	39.2
50	44.3	12.5	32.8	9.0	11.9	38.8
88	49.6	12.9	24.0	10.2	12.1	38.1
62	36.8	12.2	22.8	9.0	11.4	37.8
94	49.8	12.4	35.6	9.0	11.7	37.7
06	38.4	13.6	28.3	10.4	12.4	37.5
91	36.8	13.9	26.5	9.5	12.4	37.3
01	38.0	14.0	24.8	11.1	12.8	36.6
89	39.6	14.4	24.7	9.8	12.5	35.5
38	43.5	13.1	25.3	10.1	12.3	35.4
28	42.8	12.6	24.2	9.7	12.0	34.9
35	27.0	14.4	20.0	11.5	13.2	30.3

Interstation

Examination of the tagged selections in Figures 11 and 12 indicates the tendency for the same selections to perform in the same manner at different stations. Even though the Edmonton plots were placed on black soil and the Fallis

plots on gray soil, the points representing the various selections remained in the same general position.

The effect of soil environment was still further minimized by plotting the Edmonton yield against the Fallis protein for 1944. The regression coefficient in this case was rather low, but still highly significant, b_{py} = -.036. The more important point is the fact that this combination of data from two stations still gave a highly significant negative correlation coefficient, r_{py} = -.627. The correlation surface is presented in Figure 16. A test for non-linearity of the regression line was applied to the data, using the method outlined by Goulden (5). The regression line proved to be non-linear. The linear regression depicted in Figure 16, therefore, is not entirely correct.

The corresponding but reverse combination of Fallis yield and Edmonton protein for 1944 is plotted in Figure 17. As would be expected, these results also were highly significant. The regression coefficient is high, owing to a wide range of protein values and the narrow range of yields, b_{py} = -.086. The association between yield and protein content is good, being negative and highly significant, r_{py} = -.539.

The same procedure was carried out using the 1945 data, and gave similar results. When Edmonton yields were plotted against Fallis proteins, the scatter presented in Figure 18 was obtained. The regression coefficient is b_{py} = -.049 (highly significant). The correlation coefficient is

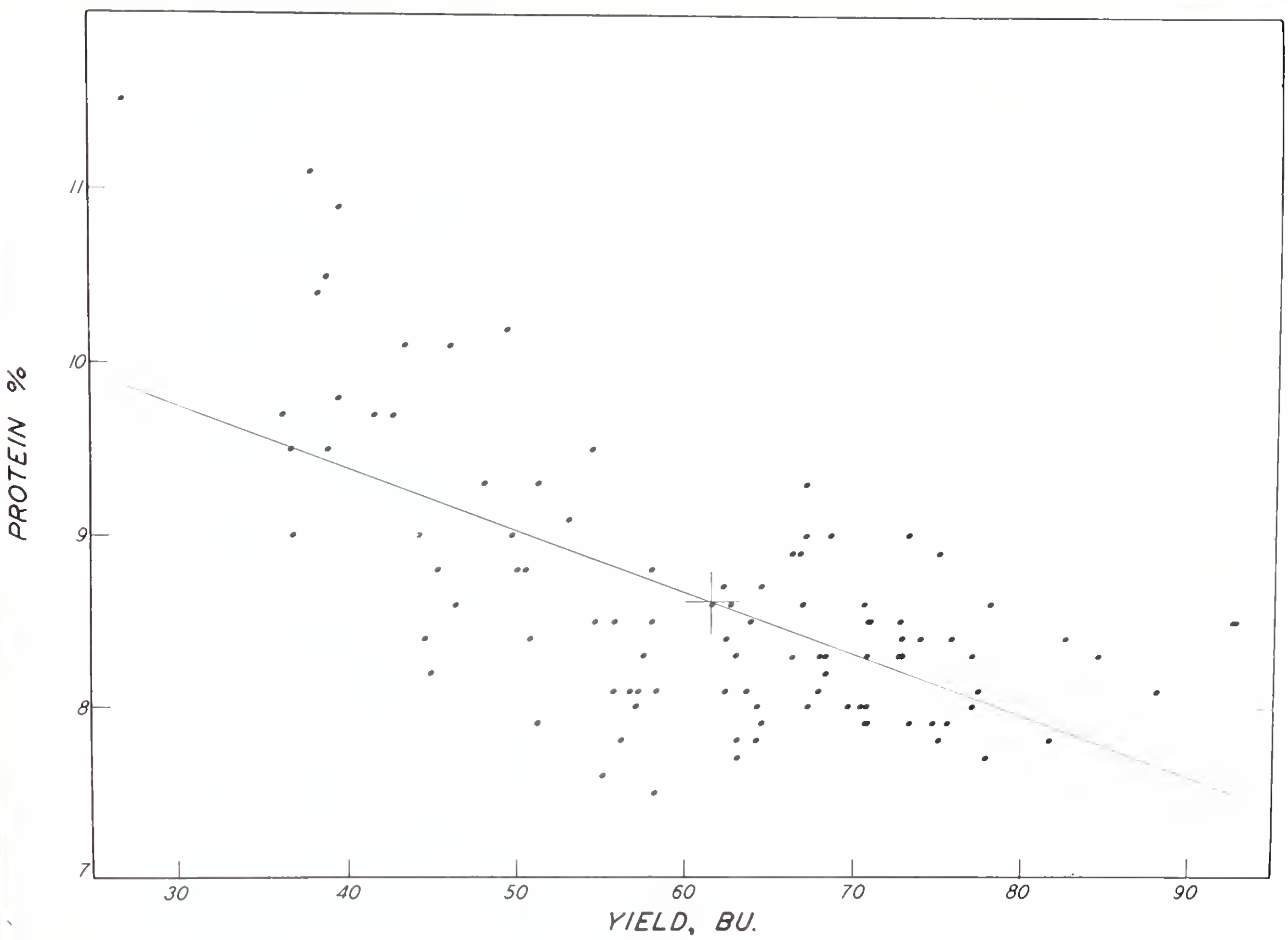

Figure 16

Relation between Edmonton yield and
Fallis protein content in the
1944 wheat tests

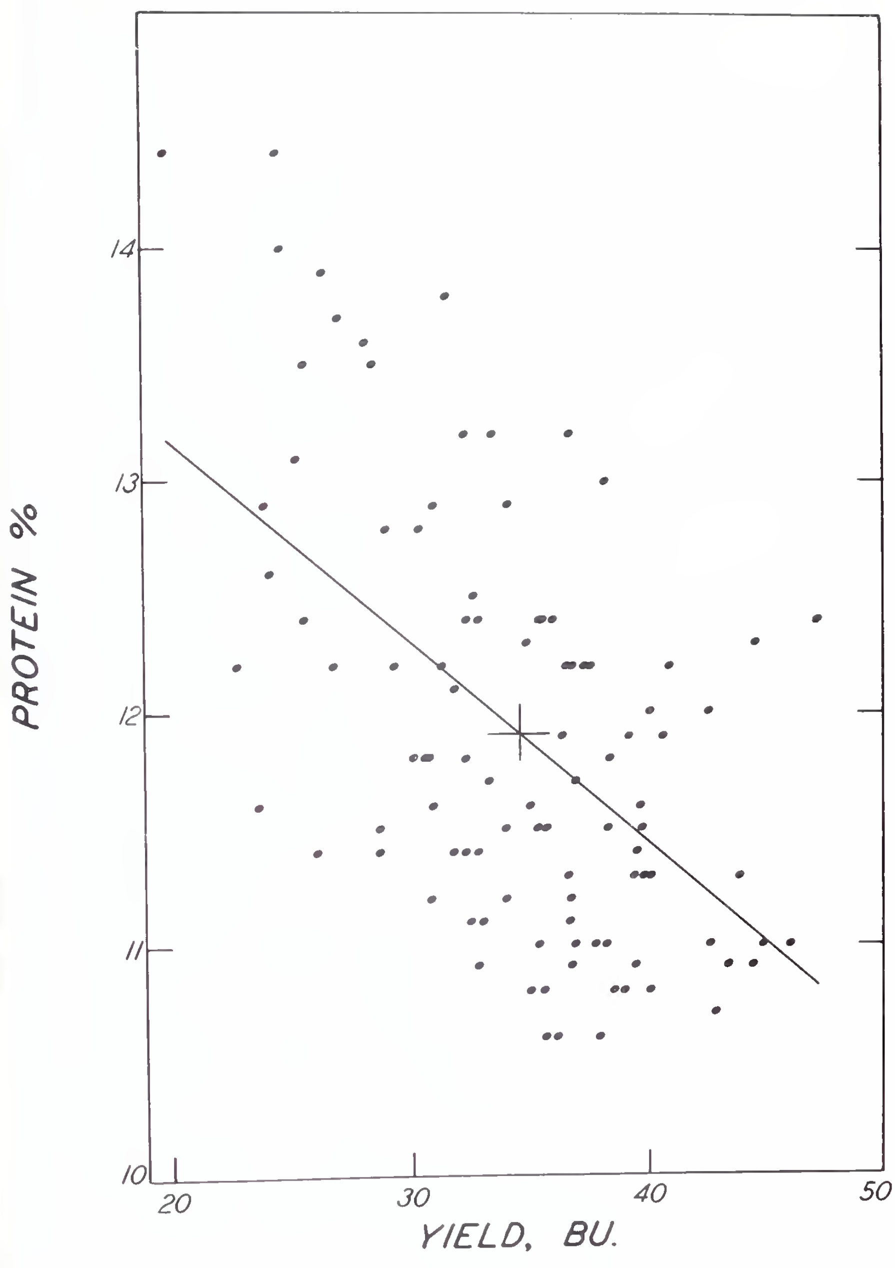

Figure 17

Relation between Fallis yield and
Edmonton protein content in
the 1944 wheat tests

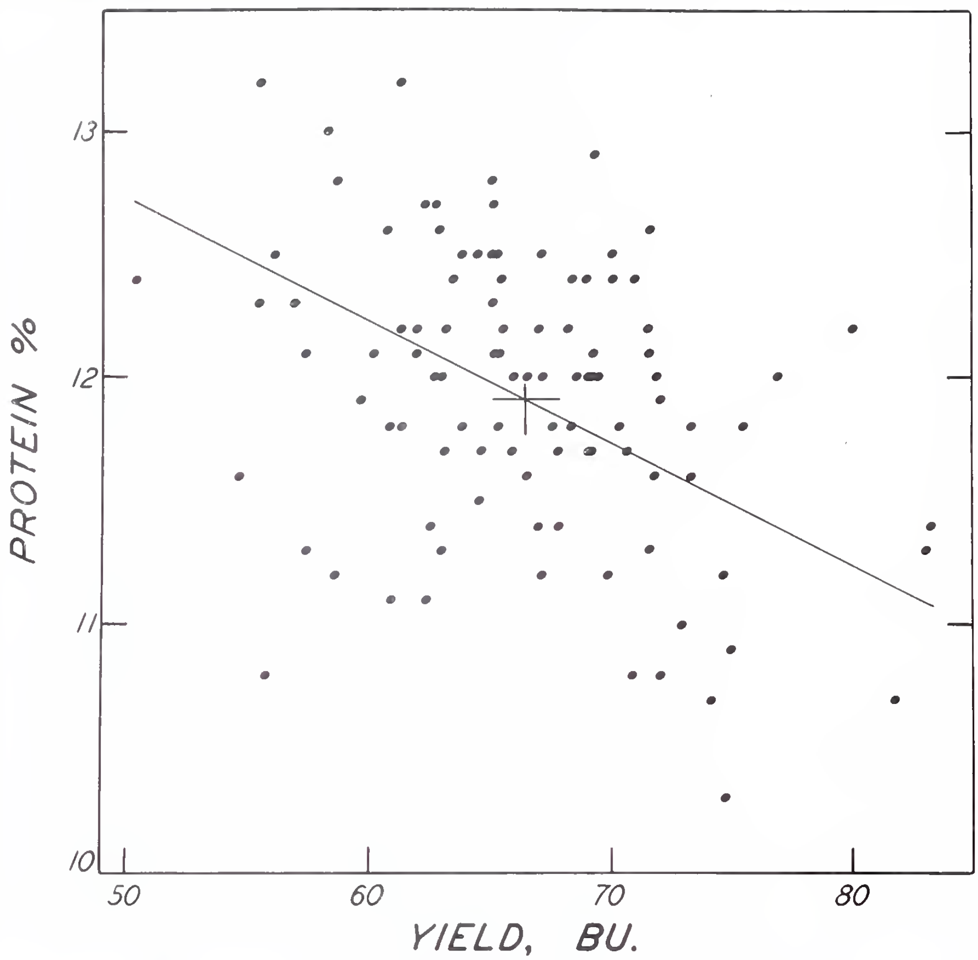

Figure 18

Relation between Edmonton yield and
Fallis protein content in
the 1945 wheat tests

also highly significant, $r_{py} = -.468$. The combination of Fallis yields with Edmonton proteins also gave highly significant results. The scatter of points is shown in Figure 19. The regression coefficient is $b_{py} = -.054$, and the correlation coefficient is $r_{py} = -.494$.

Interyear

For the Edmonton wheat test, 1944 yields were plotted against protein values for 1945. The resulting scatter (Figure 20) shows no significant trend. As would be expected, the combination of 1945 yield and 1944 protein content gives a similar result. The scatter is shown in Figure 21. The correlation coefficients, respectively, are $r_{py} = -.097$ and $rpy = -.052$, neither of which is significant. The inference is that the various selections exhibited different responses to the highly dissimilar moisture conditions of the two years. This lends support to the results obtained with interyear combinations of barley data.

Interyear combinations of Fallis data, on the other hand, show a definite trend. When 1944 yields are plotted against 1945 proteins, the scatter presented in Figure 22 is obtained. In this scatter the trend is not obvious, but a regression coefficient of -.022 and a correlation coefficient of -.218 were calculated. These figures are significant only to the 5% point.

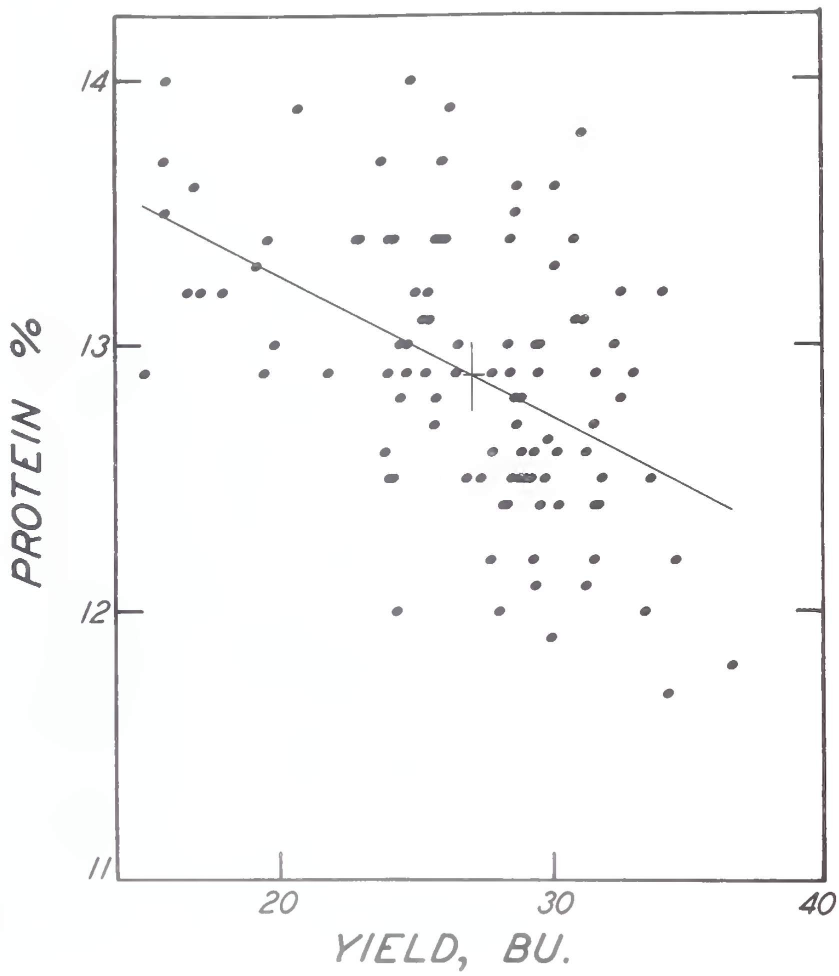

Figure 19

Relation between Fallis yield and Edmonton protein content in the 1945 wheat tests

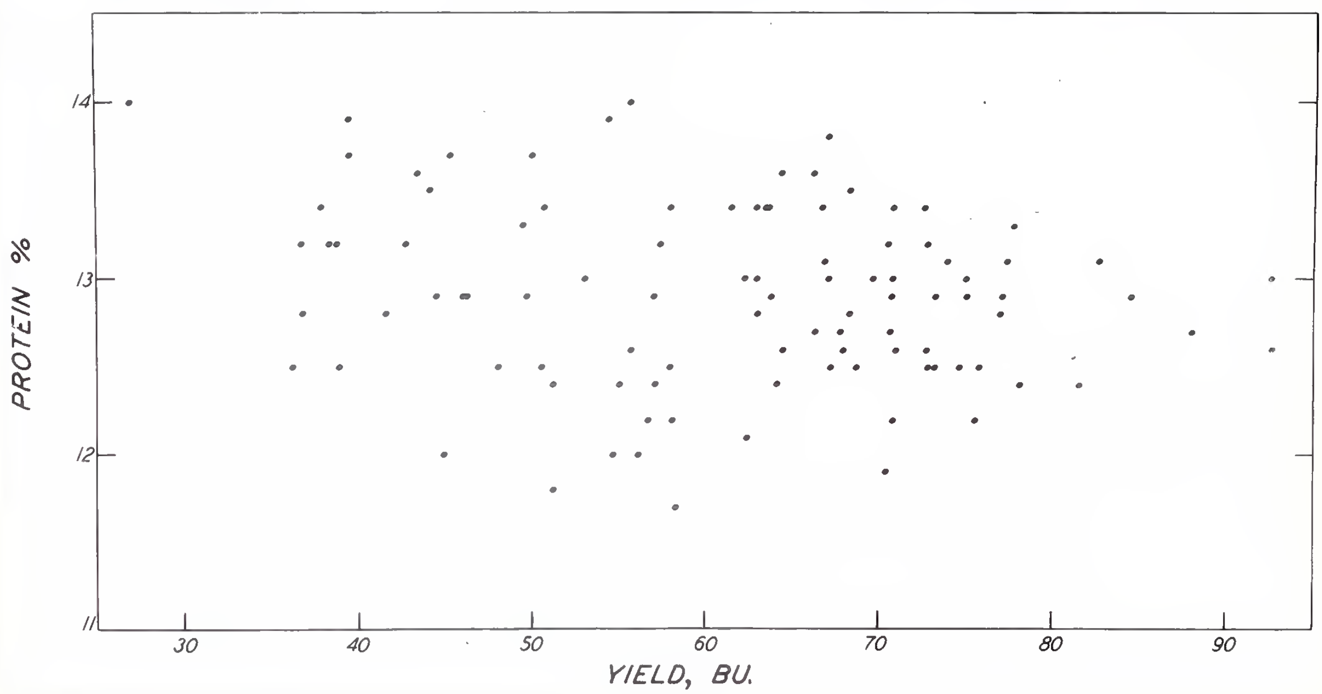

Figure 20

Relation between 1944 yield and
1945 protein content in the
Edmonton wheat tests

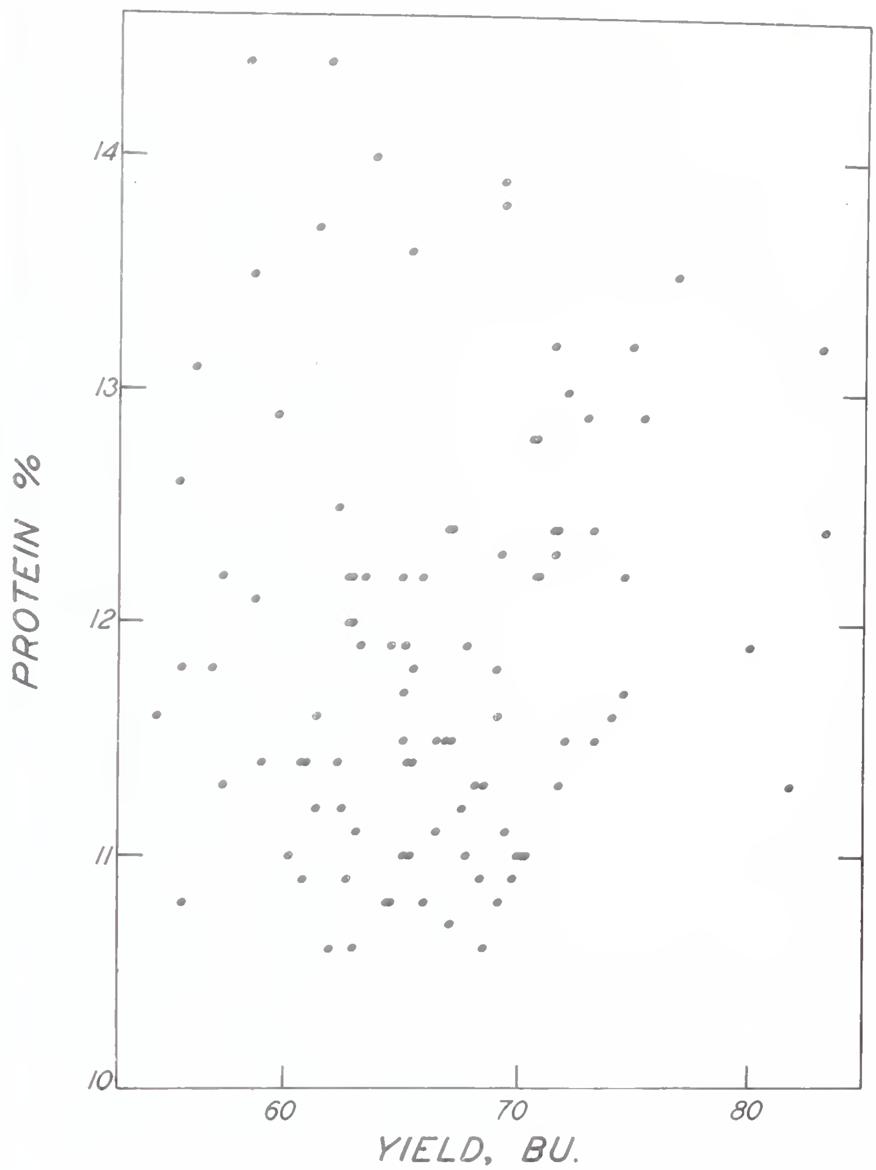

Figure 21

Relation between 1945 yield and
1944 protein content in the
Edmonton wheat tests

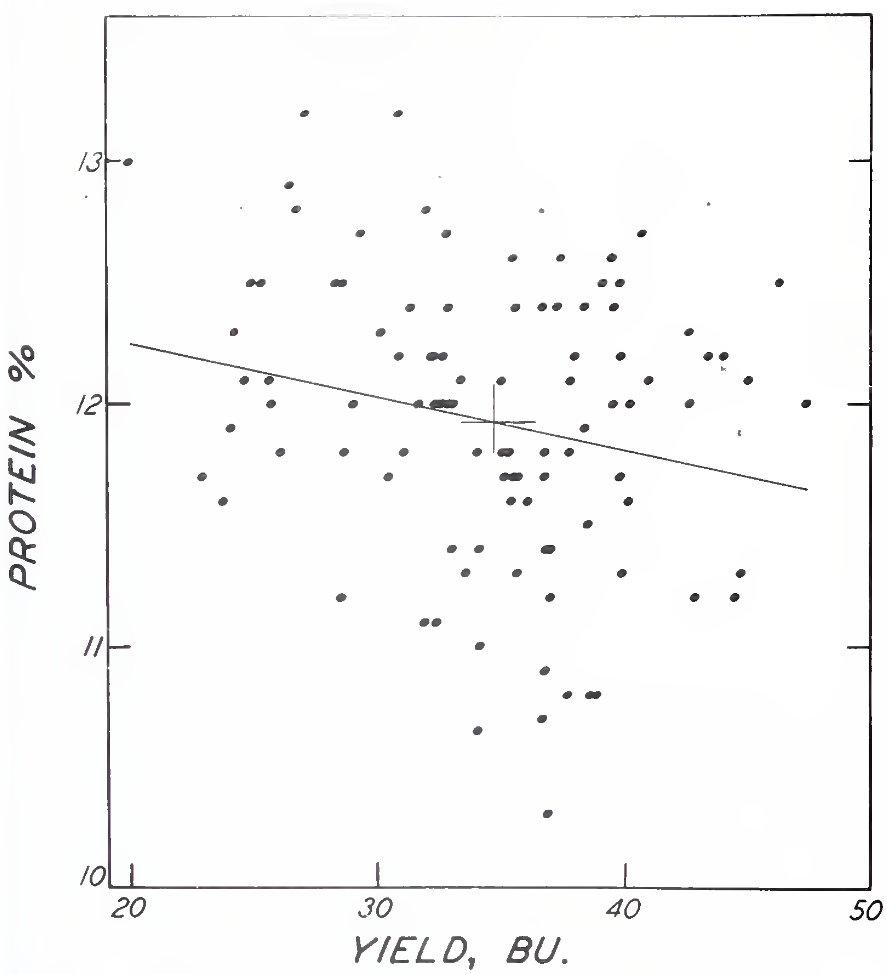

Figure 22

Relation between 1944 yield and
1945 protein content in the
Fallis wheat tests

The corresponding combination of 1945 yields with 1944 proteins gives highly significant results. The scatter of points is shown in Figure 23. The regression coefficient here is very high, b_{py} = -.103, a change in yield of only 10 bushels being accompanied by a change in protein content of 1%. The association between yield and protein content is also negative and highly significant, r_{py} = -.616.

A summary of interstation and interyear results is presented in Table X.

TABLE X

A summary of regression and correlation coefficients for interstation and interyear combinations of yield and protein data

	b_{py}	r_{py}
Interstation		
1944: Edmonton yield/Fallis protein	-.036**	-.627**
Fallis yield/Edmonton protein	-.086**	-.539**
1945: Edmonton yield/Fallis protein	-.049**	-.468**
Fallis yield/Edmonton protein	-.054**	-.494**
Interyear		
Edmonton: 1944 yield/1945 protein	-.004	-.097
1945 yield/1944 protein	+.008	+.052
Fallis: 1944 yield/1945 protein	-.022*	-.218*
1945 yield/1944 protein	-.103**	-.616**

* Exceeds the 5% point
** Exceeds the 1% point.

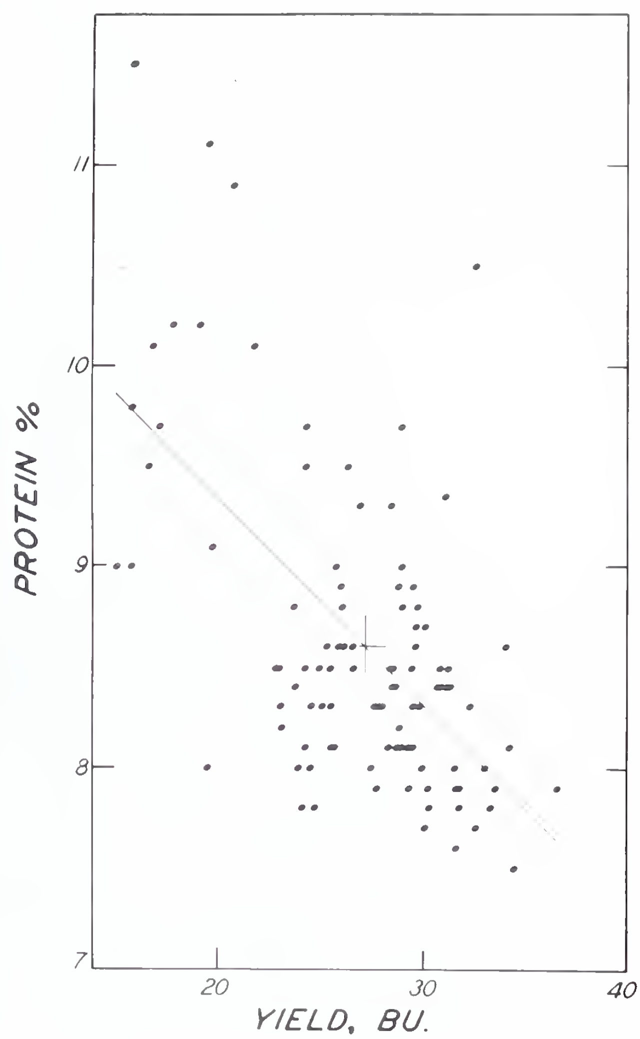

Figure 23

Relation between 1945 yield and
1944 protein content in the
Fallis wheat tests

DISCUSSION

It must be concluded from the foregoing results that a definite negative relationship exists between yield and protein content in wheat and barley. In each test, with no exception, the association was negative and highly significant. The fact that the simple correlation coefficients were highly significant in all six tests, two of which were carried out using barley selections, and four using soft wheat selections grown for two years on both black and gray soil, indicates that the association is, to a large extent, genetically controlled. Environment undoubtedly plays a part in the yield-protein relationship, but when the effect of environment is reduced by the use of interstation results, or by calculations based on mean values, the high negative correlation remains. Examination of the correlation coefficients based on the general means indicates that for both wheat and barley approximately 35 percent of the genetical potentiality for protein content is determined by yielding ability. Some type of genetical linkage is indicated for yield and protein content.

Interstation results show that the various selections give similar responses on the two soil types. This emphasizes the belief that the relationship between the two characters is largely genetically controlled, and that the characters are in some manner linked.

Interyear results are not as conclusive as those for interstation data. This leads to the belief that the ability to produce protein may be physiologically tied up with other factors. Thus, in two such widely different growing seasons as those in 1944 and 1945, the physiological balance may have been changed, leading to dissimilar responses from many of the selections during the two years. It is interesting to note that for interyear data for Fallis, where the relative scarcity of available nitrogen is more of a limiting factor than the physiological ability of the plant to make use of it, the response of each selection over the two years is more nearly alike than at Edmonton, where nitrogen is not a limiting factor of such importance.

The slope of the regression line is sufficiently steep in each case to render the negative relationship economically important. In breeding for wheat of high protein content, if a regression coefficient of -.05 can be generally expected, an increase in protein content of 1% means a loss in yield of 20 bushels per acre. Regression coefficients based on Fallis data are particularly high. Introduction of higher-yielding varieties of wheat to the gray soil zone may therefore result in even lower protein values than those now obtained.

The length of the growing period apparently exerts some influence on yielding ability. Conflicting results were

obtained for 1944 and 1945. The reason for these differences may be found in the precipitation records for the two years. In May, June, and July of 1944 over 11 inches of rain fell. During the corresponding period in 1945 the precipitation amounted to only 4.75 inches, with only 0.25 inches in the crucial month of May. The negative relationship for 1944 may be partially explained by the fact that under the influence of heavy rains the later varieties tended to lodge. The lodged spikes failed to fill as completely as those standing erect, thus leading to a decreased yield for these selections. In 1945, the selections which filled the best were those which were late in maturing, and which were therefore able to take some advantage of the late rains.

The length of the growth period also exerts some influence on the relationship between yield and protein content. This is indicated by the fact that in two tests the slope of the regression line was made steeper by holding the effect of the growth period constant. The partial correlation coefficient was also found to be greater in these two cases than the simple correlation coefficient. The multiple correlation coefficient, which expresses the combined effect of yield and growth period on protein content, was found to be highly significantly greater than the simple coefficient.

It would appear, from the foregoing statements, that the possibility of obtaining varieties which are high in both

yield and protein content is fairly remote. Such selections have occasionally been made, but the chance of obtaining them through selection work based mainly on agronomic characters is made much more difficult by the negative relationship which has now been demonstrated. This is of particular interest to the breeder of hard spring wheats and feed barleys. On the other hand, the breeder of soft wheats and malting barleys will experience little difficulty in obtaining the combination of high yield and low protein content which he desires.

It may be concluded that protein content can serve as a valuable criterion in the selection or discarding of certain strains from early-generation hybrids of wheat and barley. Protein determinations could be made on all strains which had been selected on the basis of their agronomic characteristics from head-row material. In the case of hard spring wheats, keeping the negative yield-protein relationship in mind, approximately 15% of the selections showing the highest protein content could be discarded, since their yielding ability would in all probability be very low. Approximately 15% of the selections having the lowest protein content could be discarded for this characteristic alone. For malting barley or soft wheat, approximately 35% of the selections characterized by high protein content could be discarded, since both high protein content and low yielding ability are undesirable features. A considerable saving would thus be

made in time, labor, and land, which would otherwise be used in bringing these strains up to the yield-test stage.

SUMMARY

In order to determine the relationship between yield and protein content of random selections from single crosses in wheat and barley an experiment was devised which reduced to a minimum the error due to different varieties and different environments. For each of wheat and barley a cross was made between a high-yield-low-protein parent and a low-yield-high-protein parent. After the progeny of these crosses had segregated for several generations, 100 plants were selected at random from each crop. Each lot of seed was numbered and increased during the following year. In 1944 and in 1945 these selections were grown at Edmonton in replicated yield tests. The wheat selections were also grown on the gray soil at Fallis. Records were kept of yield, protein content, and growth period for each selection.

The results of analysis of variance showed highly significant differences between selections for yield, protein content, and growth period. A highly significant negative relationship was demonstrated between yield and protein content in all six tests. The regression of yield on protein content was of such magnitude as to make this association

economically important. The effect of growth period on the yield-protein relationship was not constant enough to justify definite conclusions.

Correlation coefficients were calculated for both barley and wheat, using the mean values for protein content and yield. A highly significant negative relationship was demonstrated. Combinations of data from different stations and from different years were also used. Interstation results gave highly significant negative correlation coefficients. Interyear results showed the same general trend, though the results were not as conclusive. Methods such as these practically eliminate the effect of environment, and indicate that the yield-protein relationship is largely genetically controlled.

This negative relationship greatly decreases the chance of obtaining a high-yield-high-protein variety of either wheat or barley. The problem of selecting strains of soft wheat or malting barley is greatly simplified.

With a negative yield-protein relationship established, protein determinations carried out on head-row samples could serve as a valuable criterion for selection or discarding of many strains.

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